Light Environment in Tropical Rain Forest of Central Amazonia

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ABSTRACT

Light intensity above the groundstoreys (120 cm) and in between the ground strata of a Riverine forest, a Carrasco forest and a terra firme Rain forest was recorded through two day periods of time in the rain season (April/May) and the dry season (August) of 1969. Measurements were undertaken between 6 a.m. and 18 p.m. in minute by minute intervals (51,840 readings). The relative frequency of light intensity was computed for seven intensity classes and three periods of time per day. The spectral composition of light was determined as relative frequency of light intensities for five filter ranges of wavelengths, seven intensity classes and three periods of time per day.

The riverine forest (best light conditions for the understorey plant communities) and the terra firme Rain forest (worst conditions) developed extremely opposite positions with respect to forest light climate, while the Carrasco forest showed up with a somewhat intermediate character, but with a strong shift to terra firme Rain forest conditions.

The spectral composition of light received by the ground strata of all three forest stands was as follows: 1) light intensities peaked in the RG 630 filter range of wavelengths (5.920 Å — 7.500 Å), 2) a secondary intensity peak covered the VG 9 filter (4.420 Å — 6.440 Å) and 3) a less important secondary peak matched the BG 12 filter band (3.500 Å — 5.150 Å).

Inbetween the understorey communities, spectral light intensities were pretty low and showed another considerable red shift.

INTRODUCTION

Light is one of the important environmental factors in plant life, primarily, because of the energy supply for photosynthesis. On the other hand, light measurements in plant communities have proved to be full of difficulties. Detailed discussions on all these complex processes and techniques in tropical Rain forest all over the world are referred to by Evans (1939), Evans, Whitmore and Wong (1960), Grubb & Whitmore (1967), Schulz (1960), and many other authors. As forest structure and light climate are closely related, light environments of three forest stands in central Amazonia were comparatively studied to evaluate their characteristics away from the extremely troublesome forest inventories.

SITE DESCRIPTION

I — The Riverine forest

(Ducke Forest Reserve)

This forest community follows the small Rain forest streams, i.e. it covers the valley bottoms of the Terciary uplands of Central Amazonia. The canopy heights range from 22m to 35m, but all canopy strata are either poorly defined or not formed at all. The canopy area is shot with epiphytes, trailing lianas, Bromeliaceae and Orchidaceae. The dominant tree species belong to families, as Leguminosae, Sapotaceae and Moraceae. This forest type is referred to by Takeuchi (1961) as "Rain forest on the low terra firme". A 30m x 30m inventory recorded 57 trees (10 cm to 25 cm DBH) and 13 trees (above 25 cm DBH), including some palm trees. The crown projection areas for both diameter classes are shown in Figure 1.
The ground stratum consists of stemless palms, herbaceous plant communities and some seedlings and saplings, which form a dense ground cover. The herbaceous community was classified by Takeuchi (1961) as Hymenophyllaceae, Polypodiaceae, Lycopodiaceae, Bromeliaceae, Marantaceae, Rapateaceae, Araceae and Orchidaceae. Very common palms are: Astrocaryum sp., Oenocarpus spp., Attalea sp and Euterpe oleracea.

The soils are of the sandy riverine complex with some humus accumulation in the upper 15 cms of the soil profile. The groundwater table is quite high the year round. During, or shortly after heavy downpours, the forest floor is temporarily flooded by rain water surplus.

II — The Carrasco forest

(Ducke Forest Reserve)

The Carrasco forest under study covers a river terrace like slope of the Igarapé Barro Branco valley. The forest community must be understood as an intermediate forest stand between the terra firme Rain forest and the Riverine forest. Takeuchi (1961) described a similar forest as “inclined terra firme Rain forest” (Km 42 of the Manaus-Itacoatiara Road). The term Carrasco forest used, does not exactly match the definition of this particular forest type as refered to by Aubréville (1961).

Canopy heights range from 22m to 32m, including some emergent trees (Hymenelobium exelsum Ducke). The canopy strata are up to a certain extend well defined. The dominant tree species are Protium spp and Eschweilera spp. A 30m x 30m inventory recorded 35 trees (10cm - 25cm DBH) and 20 trees (above 25 cm DBH) respectively. The canopy projection areas of both diameter classes are shown in Figure 2. Epiphytes, Bromeliaceae and Orchidaceae are less abundant than at the Riverine Forest. The understorey consists of numerous seedlings and saplings, some herbaceous plants and very small palms.

The soils are of the latosolic complex, but contain a considerable sand fraction all over the profile.

Figure 1 — Crown projection areas of a Riverine forest at Ducke Forest Reserve, Km 26 of the Manaus-Itacoatiara Road, Central Amazonia (30 m x 30 m plot). Left: all stemdiameter classes above 25 cm DBH; all diameter classes below 25 cm DBH. • Sampling site.
The terra firme Rain forest under study is a typical climax forest of the Tertiary formations of Central Amazonia. This particular forest community cover the chapadas along the Manaus-Itacoatiara Road and was preliminary inventorized by Rodrigues (1967). The dominant tree species of the 137,000 ha forest inventory (all stem diameter classes above 25 cm DBH) are: *Eschweilera* spp. (6.5 trees/ha), *Scleronema micranthum* Ducke (3.4 trees/ha), *Corythopora alta* Knuth (2.9 trees/ha) and *Ragala spuvia* (Ducke) Aubr. (2.2 trees/ha).

Takeuchi (1961) proved, that more than 40 percent of all trees above 10 cm in diameter (DBH) belonged to three families: a) *Leguminosae*, b) *Lecythidaceae*, and c) *Sapotaceae*. The total number of trees for a 1,600 m² inventory was computed with 123 trees. These results match pretty well those of the Rodrigues inventory at least as far as families are concerned.

The dominant tree species at the “chapadas” of the Ducke Forest Reserve are *Eschweilera* spp (8.2 trees/ha) and *Scleronema micranthum* Ducke (38 trees/ha). The forest inventory covered an area of 36 ha (Aubréville, 1961).

The canopy heights range from 25m to 35m and all three strata are considerably well developed. Epiphytes, *Bromeliaceae* and *Orchidaceae* are less abundant than in the Riverine forest, but outmatch the Carrasco forest. Trailing lianas are quite common. The crown projection areas of various diameter classes are refered to in Figure 3.

The “shrub” — stratum is obviously dominated by palms, as *Astrocaryum munbaca*, *Syagrus inajai*, *Bactris* sp. et. al and various saplings. The groundstratum is covered with spots of seedlings, some stemless palms, as *Oenocarpus* spp, *Scheelea* sp., *Orbygnia spectabilis*, and a few herbs of the families *Cyperaceae*, *Marranthaceae* and *Orchidaceae*. Soils are of the heavy of very heavy latosols, which cover about 85 percent of the Tertiary uplands along the Manaus-Itacoatiara Road (IPEAN, 1969).

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Figure 2 — Crown projection areas of a Carrasco forest at Ducke Forest Reserve, Km 26 of the Manaus-Itacoatiara Road, Central Amazonia (30 m x 30 m plot). Left: all stem diameter classes above 25 cm DBH; Right: all stem diameter classes below 25 cm DBH. • Sampling site.
All three stands are extremely heterogenous and so far, difficult to handle with as far as representativeness of some small plots for the total are concerned. This fact should be always under consideration when data evaluation are discussed in this paper.

INSTRUMENTS AND METHODS

Incident direct, scattered and transmitted light in the forest stands was recorded by two Standard Lux Meter II, provided with high quality taut supension band systems and range selector switches for 0 — 100 Lux and 0 — 1,000 Lux.

The Standard Lux Meter II were connected with six selenium elements S60 in spray — waterproof housings. Both, the Standard Lux Meter II and the selenium elements S60 were calibrated in the laboratory.

The selenium elements S60 used were sensitive for the frequency range 3.500 Å to 7.200 Å of the electromagnetic spectrum; i.e. the receptors cover practically the entire range of wavelengths with importance in plant physiology.

About 120 cm above the forest floor, the selenium elements S60 were mounted face up on tripods. One element measured total light intensity at the above level, supplied with a clipped-on platinum opaque filter (light absorbance: 1:10) whenever necessary. The spectral distribution of light intensities was recorded by five elements with clipped-on glass filters. The filters used are: BG 12, VG 9, RG 630, RG 665 and RGN 9. Detailed information about relative transmittance of the above filters, etc. is referred to by Jenaer Glaswerke Schott (1962).

Two day periods of measurements for each stand were undertaken in April and May, 1969 (rain season) and August, 1969 (dry season) between 6 a.m. and 18 p.m. minute by minute (51,840 readings over all). All light measurements were related to: 1) full direct and scattered sunlight, including hazy conditions (reduced direct, but full scattered light) and 2) scattered light (sun behind dense...
The overcast was estimated in fraction of one tenth, simultaneously with light measurements. These estimates are rather tentative because of the limited view.

**Fellow Review**

The light climate in a forest is usually expressed as a percentage of total light intensity in the open; i.e. the light interception capacity of the canopy strata is determined (daylight factor according to Atkins, et. al. (1937)).

Light climate studies on tropical forest communities all over the world are referred to by Schulz (1960). Light climate of a montane and lowland forest in Ecuador was comparatively studied by Grubb & Whitmore (1967).

For the Amazon basin, forest light readings were taken by Ashton (1958) near Santarém in a probably old secondary Rain forest. Kanwisher (3) (1967) stated the daylight factor of the Amazonian Rain forest to be in the order of 4. to 8. percent. Alvim (3) (1967) calculated the average light intensity for a Rain forest near the Rio Negro — Rio Branco junction with 1.35 percent. Coutinho, Lambert (3) (1967) reported the daylight factor for a terra firme Rain forest to be 0.5 to 1.0 percent. Comprehensive light climate evaluations by Loomis, Williams and Moraes (1967) recorded the daylight factor for two terra firme Rain forest sites near Belém with 1.1 percent and 1.5 percent, for a secondary forest (capoeira) with 1.8 percent, for an Igapó transect with 3.7 percent and for a varzea forest community with 1.0 percent. Williams (3) et. al. (1967) studied the light environment of a flooded forest (Igapó) and a terra firme Rain forest near the confluence of the Rio Negro with the Rio Branco. The penetrating light intensity was 4.2 percent and 1.1 percent, respectively. Brinkmann (1970d) reported the daylight factor for a dense capoeira near Manaus with 0.7 to 1.9 percent, while the “spectral” daylight factor was: BG 12 — 0.7; VG 9 — 1.1; RG 630 — 1.5; RG 665 — 2.6 and RGN 9 — 3.0 (3 day average).

All these evaluations confirm the fact, that daylight factor is really of little use in comparative studies on various forest communities because the fractionizing effect is to small to be significant. On the other hand, the ratio total light (open) to total light (forest) has no ecological meaning at all.

**RESULTS AND DISCUSSION**

The evaluation of light intensities as an important ecological complex in forest life and natural forest regeneration cycles has to answer to following questions: 1) which total light and spectral light intensities are supplied to a particular forest stratum? and 2) how are these light intensities distributed over time?

The complex vertical structure and heterogeneity of the tropical Rain forest sites under study, as well as the short time variations of total light intensity above the canopies, and in consequence in the stands, required the great population of light measurements (total readings: 51,840), to define the particular light climate at the particular forest plot. All available light intensities at about 120 cm above the ground of all three sites were recorded by scanning the random light surplus gradually from deep shade light to full direct sunlight (sunflecks). The appropriate statistical evaluation of the obtained data populations was the relative frequency distribution of light intensities, as “abnormally” high sunfleck readings did not carry undue weight.

The relative frequencies of light intensities for all three forest stands, as 1) the Riverine forest, 2) the Carrasco forest, and 3) the terra firme Rain forest were computed for seven intensity classes and three periods of time per day (see Table 1).

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The evaluation of all results presented in Table 1 confirm the well developed individuality of the three forest stands, as far as light climates are concerned. While the Riverine forest (best light conditions) and the terra firme Rain forest (worst light conditions) show extremely opposite positions, the Carrasco forest has an intermediate character, but with a very strong shift to the terra firme Rain forest conditions, i.e. the latter forest types are similar structured.

Between 6 a.m. and 10 a.m. 94 percent of all light readings at the terra firme Rain forest site are below the 200 Lux level, while the corresponding percentages for the Carrasco forest and Riverine forest are 63 percent and 36 percent. A similar, but less extreme situation was calculated for the period of time between 14 p.m. and 18 p.m., the corresponding percentages are 66 percent, 71 percent and 34 percent. Minimum conditions for the photosynthetic response of various plants of the ground stratum are assumed to be at about 200 Lux. Very short bursts of intensive light (sunflecks), which are scarcely important for the CO₂ assimilation of the plants are recorded for the terra firme Rain forest (morning: no event; afternoon: 1 percent) and the Carrasco forest (morning: 5 percent; afternoon: 1 percent). As a matter of fact, these minimum conditions are one of the growth rate regulatives of the groundstratum, a selective principle for species present, but at no time a mass development restriction for seedlings and saplings. These assumptions match pretty well growth rate determinations by Pires (1966). The growth rates for saplings in the ground stratum of a terra firme Rain forest site near Belém were extremely low. The same was observed by Vieira (verbal communication) for rosewood saplings at a terra firme Rain forest plot near Santarém. Rosewood saplings of the understorey with thirty five years of age were about 60 cm high. The 200 Lux photosynthetic response limit for understorey plants cannot be generalized, but is rather significant. Only some species (some tree seedlings and obviously some herbs) of the ground stratum have lower compensation.

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| TABLE 1 — Relative frequency of light intensities above the ground stratum (120cm) of (1) a Riverine forest; 2) a Carrasco forest and 3) a terra firme Rain forest (Ducke Forest Reserve, central Amazonia) for seven intensity classes and three periods of time per day.
points than 200 Lux. Coutinho, Lamber-
ti (1967) reported on some investigations
at a terra firme Rain forest near the Rio Ne-
gro — Rio Branco junction, where plants of
the understorey photosynthesized in the early
morning just below the 200 Lux level.

Even between 10 a.m. and 14 p.m., the
terra firme Rain forest (15 percent) and the
Carrasco forest (8 percent) reported light
intensities below 200 Lux. Above the 500
Lux level, the relative intensity frequencies
were characteristical for the particular forest
types (Riverine forest — 92 percent; Carras-
co forest (23 percent), and terra firme Rain
forest (4 percent). The ecological meaning
of these results are quite significant. While
the Riverine forest received a more or less
continuous light surplus during the four hours
period of time, the terra firme Rain forest
was flashed occasionally by intensive light
bursts (sunflecks). Although the percentage
for the Carrasco forest is considerably higher,
only a small fraction of the light surplus are
longer lasting sunflecks. According to Schulz
(1960) at higher light intensities the photo-
synthetical response of the plants tends to
approach a constant value far below the maxi-
mum intensity. This fact reduces sunfleck
light efficiency to a very minimum. On the
other hand, at low intensity levels the photo-
synthetical response of many plants is some-
what proportional to light intensity, i.e. that
for the terra firme Rain forest and up to some
extent for the Carrasco forest assimilation
processes are prevalingly limited to the 10
a.m. to 14 p.m. period of time (see Table 1).

Sunfleck intensities change rapidly. Read-
ings as high as 45,000 Lux were obtained
for the Riverine forest. The maximum sun-
fleck intensity recorded for the Carrasco
forest and the terra firme Rain forest were
12,000 Lux and 5,800 Lux respectively.
According to Alvim (1967) readings as high
as 60,000 — 80,000 Lux could sometimes
be obtained.

When sunfleck light lasted long enough
seedlings of several tree species at a Suriname
Rain forest site were observed to grow vigor-
ously. (Schulz, 1960). The seedlings cover-
ed a patch in the forest which received direct
sunlight through a small hole in the canopy
during about 40 minutes per day. For the rest
of the day light intensity was about the same
as in neighbouring spot.

Following the light climate analyses
stated above, the most significant event in
the tropical Rain forest is the collapse of large
emergent trees. According to Schulz (1960)
seedlings and saplings of a number of tree
species reach their maximum growth rates
when exposed to full sun light. An intensive,
but qualitative study on the factor light as a
basic element in tree growth at the Ducke
Forest Reserve was carried out by Araujo
(1970). Maximum growth rates in full sun
light were recorded for: Carapa guianensis
Aubl., Cedrelina cataeaeformis Ducke, Calo-
phyllum brasiliense Com., Jacaranda copaia
(Aubl.) D. Don and Bayassa guianense Aubl.
Survival of species depends therefore on a
serious “forest accident”, which opens the
canopies, and great amounts of seedlings in
waiting position, i.e. a high reproductive
capacity.

Coincidently with light intensity
measurements spectral light intensity readings
were taken to compute the spectral compo-
sition of the forest light climates. For all
three forest sites under study, the spectral
light intensities for five filter ranges, seven
intensity classes and three periods of time per
day were calculated as relative frequencies
of spectral light intensities (see Table 2).

The evaluation of spectral light intensi-
ties obtained for all three forest types (Ta-
ble 2), confirm the following suggestions:
1) light intensity peaked in the filter RG 630
range of wavelengths (5.920 Å — 7.500 Å), 2)
a secondary intensity peak covered the filter
VG 9 region (4.420 Å — 6.440 Å) and, 3) a
less pronounced secondary peak matched the
filter EG 12 range of wavelengths (3.550 Å —
5.150 Å). Between 6 a.m. and 10 a.m. the
intensity of spectral light for all filter regions
is almost completely below 300 Lux. The differ-
### Table 2: Relative Frequency of Spectral Light Intensities above the Ground Stratum (120 cm) of 1) a Riverine Forest, 2) a Carrasco Forest and 3) a Terra Firme Rain Forest (Ducke Forest Reserve), Central Amazonia for Five Filter Ranges of Wavelengths, Seven Intensity Classes and Three Periods of Time per Day.

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The light intensity levels for both particular filter regions were quite similar and low. For both filter bands, the light interception by the canopy strata of the Carrasco forest and terra firme Rain forest increased slightly, but decreased extremely for the Riverine forest, where about 95 percent (BG 12 — 98%; VG 9 — 94%) of all light measurements were above the 200 Lux level. As shown above (Table 1), the well formed and dense canopy strata of the Carrasco forest and the terra firme Rain forest cut out widely the blue fraction of the spectrum, i.e. direct and scattered sunlight. On the other hand, the hardly defined canopy strata of the Riverine forest, perforated by gaps and openings, was widely open for diffuse skylight and bright sunflecks.

The light climate of the Riverine forest, the Carrasco forest and the terra firme Rain forest about 120 cm above the forest floor was studied and analyzed above, i.e. the total light intensity and the spectral composition of light received by the understorey plant communities. The following light intensity determinations were undertaken to evaluate the spectral composition of light in-between the ground strata of all the forest types under minimum conditions, i.e. days without or mostly without full direct sunlight. Scattered light in the groundstorey was measured by means of five selenium elements S60, mounted face down on tripods about 120 cm above the forest floor. The spectral composition of understorey light climate was studied by clipped-on glass filters as used above. Readings were done in five minute intervals over a three days period of time during the rain season of 1969 (May) for all three forest types. The vegetation of the ground strata was tentatively inventorized by 10 plots on a 2m x 2m grid. These plots were selected at random around the sampling stations. Up to 100 cm height all plants were sampled and fractionized into: 1) palm communities, 2) herbaceous plant communities, and 3) seedlings and saplings (see Table 3).
The Riverine forest had about twice as much palms in the ground stratum as the Carrasco forest or the terra firme Rain forest, which did not show any great differences in the total number. The same distribution pattern showed up with the herbaceous plant community, only that the Riverine forest reported about five times as much herbs. Seedlings and saplings were the dominant fraction of groundstorey vegetation for the Carrasco forest and the terra firme Rain forest (five to ten times higher in total number of plants than counted for the herb, and palm communities). The abundance of seedlings and saplings on the waiting list indicate the high potential reproductive capacity of these forest types, where light is the key factor to release the suppressed ground stratum communities.

During the periods of readings the sky was completely covered with clouds and no sunflecks were observed on the ground. Every day, some rain was recorded.
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<td>BG 12</td>
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<td></td>
<td></td>
<td>RG 630</td>
<td>14 83 1</td>
<td>75 24 1</td>
<td>20 31 45 3 1</td>
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<tr>
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<td>RG 665</td>
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<td>RG 630</td>
<td>42 58</td>
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**TABLE 4** — Relative frequency of spectral light intensities in the ground stratum of 1) a Riverine forest, 2) a Carrasco forest and 3) a terra firme Rain forest (Ducke Forest Reserve, central Amazonia), for five filter ranges of wavelengths, six intensity classes and three periods of time per day.
For all three forest stands under observation, the spectral light intensities in the understory plant communities were calculated as relative frequencies for five filter ranges of wavelengths, six intensity classes and three periods of time per day (see Table 4).

Just the RG 630 filter range of wavelengths (5.920 Å — 7.500 Å) reported light intensities above 30 Lux, i.e. under minimum light conditions the light climate inbetween the ground strata of all three forest communities was obviously uniform and light intensities were extremely low. The understory plant communities of the Carrasco forest and the terra firme Rain forest, were liable to a serious light stress; consequently leaf formation and growth rates were concerned. According to Alvim (1964), these morphogenic effects are superexposed by a phytochrome response, i.e. plants of the ground stratum are “short-day” exposed not only due to reduced light intensities during morning and afternoon, but also to higher proportions of far-red in the shaded habitat.

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RESUMO

O Autor apresenta um estudo comparativo do fator “luz” em três tipos de floresta na região central da Amazônia: floresta ribeirinha (floresta da baixa terra firme), carrasco e mata primária.

São discutidas as dificuldades e a complexidade do problema enfatizando-se a importância das correlações entre luz e estrutura da floresta.

É caracterizado o equipamento utilizado e descrito o procedimento seguido para a determinação da intensidade luminosa total, utilizando-se diferentes filtros em 51.840 determinações durante a estação chuvosa e a estação seca, procurando verificar a intensidade luminosa total e espectral em cada stratum e como são aquelas intensidades distribuídas no tempo.

A frequência relativa da intensidade luminosa foi computada em sete classes de intensidade e três períodos de tempo por dia. A composição espectral da luz foi determinada como frequência relativa de intensidades por meio de filtros para cinco faixas de comprimento de ondas.

Na floresta ribeirinha foram encontradas as melhores condições de luz e na mata primária foram registrados os valores luminosos mais baixos. O carrasco ocupa uma posição intermediária, com nítida tendência às condições encontradas na mata primária.

Quanto à composição espectral da luz recebida pelo stratum ao nível do solo nos três tipos de floresta, foi encontrado um pico de intensidade na faixa 5.950 Å — 7.500 Å, um pico secundário entre 4.420 e 6.440 Å e um terceiro pico, menos importante, entre 3.500 a 5.150 Å.

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